Morphology of Antennal Gustatory Sensilla and Glands in Some Parasitoid Hymenoptera With Hypothesis on Their Role in Sex and Host Recognition

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Abstract.—On the basis of scanning and transmission ultrastructural investigations of nine species of parasitoids in four superfamilies along with scanning data on seven other species in three additional superfamilies, several new sensory and secretory antennal structures are defined. These are: uniporous gustatory sensilla (UGS), multiporous gustatory sensilla (MGS), male ventral (MVG) and lateral (MLG) glands, male and female dorsal gland (MDG, FDG), and accessory glands (AG) associated with MGS. Using these structures, two functional areas, "touch and taste area" and "release and spread area", are proposed in an attempt to associate them with behavior and to clear some nomenclatural problems in different taxa. It is suggested that the role of these areas is chemical communication during sexual and host recognition. Limited observations indicate that non-parasitoid Aculeata also have some of these structures.

INTRODUCTION

The antennae of parasitic Hymenoptera are segmented appendages that have been subdivided in various ways. Although the antennae consist of a series of segments, we prefer the term antennomer. Most commonly the antennae are divided into scape with radicula, pedicel, anelli and flagellum (Fig. 1a) (e.g. Boucek 1988). However, these can often be further subdivided based on the modification of several antennomers. For example, often the distal antennomers are enlarged forming a clava with the remainder being called the funicle. This situation is common in females, but in certain taxa may also occur in males.

In general these various labeled antennomers are numbered according to the smaller subdivision resulting in, for example (Fig. 1a), six funicular antennomers and three claval antennomers. However, using such a system becomes cumbersome when comparing the morphology and function of the various antennomers be-

tween the sexes or between species, or in consideration of the evolutionary relationships of the various antennomers in different groups.

Another common system numbers the antennomeres consecutively from the scape or first antennomere (A1), pedicel (A2) and so on (Fig. 1b) and is followed here for the sake of uniformity and simplicity. For the same reason, but especially for the still controversial opinions about the true structure of anelli (Richards 1956; Graham 1969; Schauff 1986; Boucek 1988; Hayat 1990; Gauld and Bolton 1988), they are not numbered here.

Traditionally the antennae have been described as sensory appendages which may support a large number of sensilla of different types (Miller 1972; Richerson *et al.* 1972; Weseloh 1972; Voegele *et al.* 1975; Borden *et al.* 1978; Barlin and Vinson 1981; Cave and Gaylor, 1987; Bin *et al.* 1989; Navasero and Elzen 1991; Olson and Andow 1993). Using external features many different names have been proposed, possibly for the same type of structure, or in-
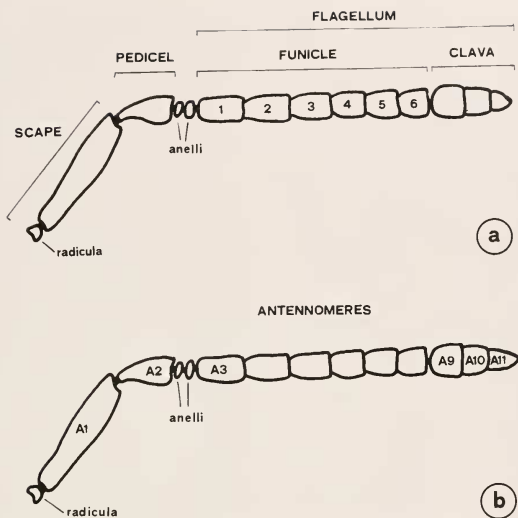
Fig. 1. Comparison of the different types of antennal terminology: a) traditionally used; b) adopted in the text.

versely one name may cover different structures, so causing confusion in the literature. Only through the study of internal details can the sensilla and associated structures be correctly defined and relatively few of these structures have been so studied with many others still to be investigated.

This has become more apparent as ultrastructural studies have revealed that some obvious features, as well as inconspicuous or obscured features and structures, thought to be sensilla, were actually release sites of glands (Dahms 1984; Bin and Vinson 1986; Bin et al. 1989; Pedata et al. 1993; Isidoro and Bin 1995). One other recent aspect is that some glands and sensilla can be in close association (Bin et al. 1989).

In this study only the sensory and secretory structures that probably come into contact for chemical communication during sexual and host recognition have been investigated. We provide new anatomical evidence for the function of some of the antennal structures. We also make comparisons among different taxa, reinterpret the functions of antennae in some groups of parasitoids, relating some of the structures to behavior. Some information on the Aculeata is included.

MATERIALS AND METHODS

The insects examined in this study are presented in Table 1. For scanning electron microscopy (S.E.M.) observations, males and females were anesthetized in CO_2, beheaded, and immediately im-

Table 1. The antennae of the species and sex examined with SEM and TEM are presented

Taxa	Sex	SEM	TEM
Ichneumonoidea			
Ichneumonidae			
Cylloceria melancholica Gravenhorst	♂	+	
Ichneumon sarcitorius L.	♂	+	
Pimpla hypocondriaca (Retzius)	♂	+	
Proctotrupoidea			
Diapriidae			
Trichopria (?*drosophilae*) (Perkins)	♂ ♀	+	+
Coptera occidentalis (Muesebeck)	♂ ♀	+	+
Ceraphronoidea			
Ceraphronidae			
Aphanogmus steinitzi Priesner	♀	+	
Chalcidoidea			
Aphelinidae			
Encarsia asterobemisiae (Vigg. & Mazz.)	♀	+	+
Mymaridae			
Polynema striaticorne (Girault)	♀	+	
Trichogrammatidae			
Trichogramma brassicae (Bedzenko)	♀	+	+
Platygastroidea			
Platygastridae			
Amitus spiniferus (Brethes)	♂ ♀	+	+
Scelionidae			
Mantibaria anomala Dodd	♀	+	+
Telenomus chloropus (Thomson)	♀	+	
Trissolcus basalis (Wollaston)	♂ ♀	+	+
Trissolcus simoni (Mayr)	♀	+	+
Chrysidoidea			
Dryinidae			
Neodryinus typhlocybae (Ashmead)	♀	+	+
Vespoidea			
Vespidae			
Vespa crabro (L.)	♂	+	

mersed in 50% ethanol solution and kept overnight at 4°C. After dehydration in a graded ethanol series, the heads with antennae were critical point-dried in a Balzers Union CPD 020 unit, gold coated in a Balzers Union SCD 040 unit, and finally examined with Philips 501 B, Philips XL 20 and Jeol JSM 35. In some cases specimens were previously treated with Neutrase to remove secretions from the sensilla or with KOH to remove the internal tissues to reveal additional release and spread structures (Bin and Vinson 1986).

The semi-schematic tridimensional drawings represent the results of transmission electron microscopy observations, either published (Bin *et al.* 1989; Isidoro and Bin 1995; Pedata *et al.* 1995) or "in preparation".

RESULTS

GUSTATORY SENSILLA

Based on both external and internal morphology there is a group of sensilla that are relatively thick walled and have either one, or rarely a few, apical pores (uniporous) or have a numbers of pores

(multiporous) distributed on an area that varies in shape and size (Altner and Prillinger 1980; Zacharuk 1985). Further, these sensilla are only located in areas that are associated with touching the substrate, host or opposite sex (Weseloh 1972; Norton and Vinson 1974b; Bin' et al. 1988; Vinson et al. 1988). For these reasons we have considered these sensilla as gustatory.

Uniporous Gustatory Sensilla (UGS)

These are typical sensilla chaetica, generally long, straight antennal setae (hairs) that stick out (Fig. 2a–b). These sensilla have a fluted setal shaft tapering from the base to the rounded uniporous tip (Fig. 2c). The cuticular wall is relatively thick. The UGS are present in both sexes and are either clustered at the apical antennomere or latero-ventrally in several antennomeres (Figs. 2, 3 a–c). The cellular components consist of three sheath cells (techogen, tormogen and trichogen) and five sensory neurons, 4 of which are chemoreceptors. The 4 dendrites reaching unbranched to the apical pore with the 5th one functioning as a mechanoreceptor (Fig. 3d). Therefore, we suggest that the UGS respond not only to chemicals acting on contact, but also respond to mechanical stimuli. These common ultrastructural features have been ascertained in Trissolcus basalis (Bin et al. 1989), Amitus spiniferus and Encarsia asterobemisiae (in preparation).

We suggested that sensilla with a similar external appearance and location, commonly reported in different taxa, but referred to with different names, can be referred to as uniporous gustatory sensilla. Some examples are the thick walled pegs (Slifer 1969), sensilla chaetica (Miller 1972; Wibel 1984; Bin et al. 1989), and fluted basiconic sensilla (Norton and Vinson 1974a, 1974b; Navasero and Elzen 1991) described from various parasitic species.

Multiporous Gustatory Sensilla (MGS)

These are present ventrally only in females and their shape, number and pattern per antennomere varies remarkably within different groups. The multiporous area is also variable in shape and size. In Trissolcus basalis the MGS appear as basiconic sensilla and occur in longitudinal pairs on several antennomeres, A7-A10, except the apical one, A11, which has only one (Fig. 4a). The cuticular apparatus consists of a short, conical peg inserted in a narrow shallow pit and terminating in an elongated sub-elliptical multiporous area with 7–8 transverse ridges grooved on the top. Each ridge consists of 4–7 lifetable lobes which cover a thin multiporous lamina (Fig. 5b). The multiporous area is generally covered with a secretion (Fig. 4b), from accessory glands (see below), which can be removed by a protease treatment (Fig. 4c). The cellular components consists of three well developed sheath cells enveloping a very high number of sensory neurons, about 420 (Fig. 5a). The perikaryons occupy most of the antennomere volume while outer dendritic segments, gradually tapering to the tip, end unbranched near the pores present on the multiporous area (Fig. 5b). In another scelionid, Mantibaria anomala, 3 or 4 MGS, with a conical shape and a smaller multiporous area innervated by 120 sensory neurons, are present on the apical antennomere (Fig. 4 d–e). No accessory glands are found in this species (in preparation).

In the platygastrid Amitus spiniferus the MGS are distributed in a similar way to Trissolcus basalis but in a smaller number. One is present on A8 and A10 and 2 on A9 (Fig. 4 f-g). However these are deprived of the accessory glands. Further, the multiporous area is smaller and only innervated by 220 sensory neurons (in preparation).

In Trichogramma brassicae there are about 20 MGS distributed on the distal half of the apical antennomere (Fig. 6a). Externally they resemble recurved sensilla trichoidea and are laterally flattened (Fig. 6b) with numerous pores located along the sharp outer margin of the distal half of the sensillum (Fig. 7). Each sensillum is inner-
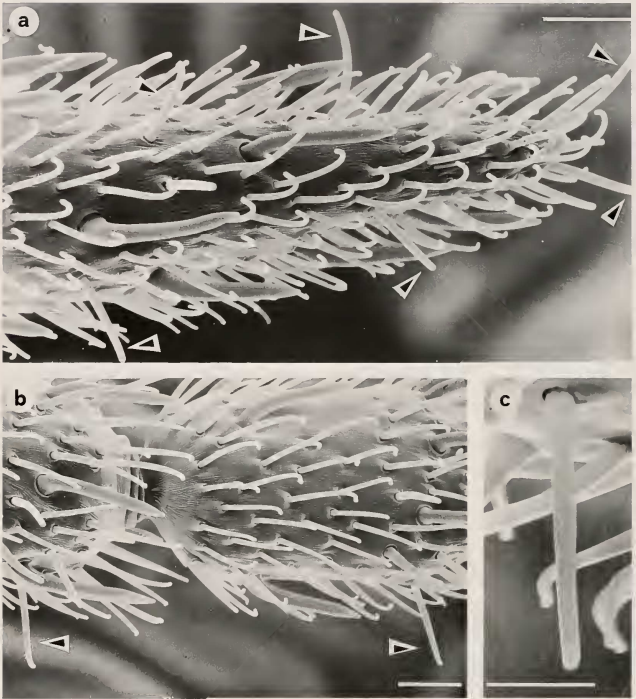
Fig. 2. Uniporous gustatory sensilla (arrows), an example in *Trissolcus basalis* male: a) clustered on apical antennomere, b) ventro-laterally located on other antennomeres, c) detail. (bars: a and b = 10 micron, c = 5 micron).

vated with 10 sensory neurons, with the outer dendritic segments running naked along the shaft lumen to reach the pores where some of them branch (Fig. 7).

In *Trichopria* sp. (probably *drosophilae*), A11 and A12 have about 20 and 40 MGS respectively, distributed in a large patch and interspersed with tactile hairs (Fig. 8a,

b). Each MGS is innervated by 5 sensory neurons. Only A12 presents a ventral accessory gland (in preparation).

GLANDS

Antennal glands were first discovered in the antennae of male parasitoids (Dahms 1984, Bin and Vinson 1986; Pedata
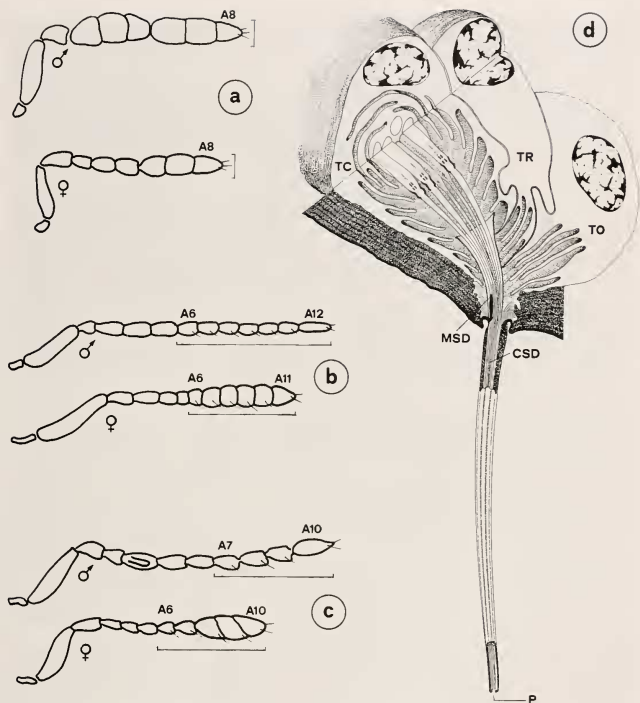
Fig. 3. Distribution of uniporous gustatory sensilla (arrows) on males and females of three different species showing some differences in location: a) *Encarsia asterobemisiae*, b) *Trissolcus basalis*, c) *Amitus spiniferus*. A diagram of a Uniporous Gustatory Sensillum based on data from *Trissolcus basalis* (d): CSD, chemosensory dendrites; MSD, mechanosensory dendrites; P, pore; TC, techogen cell; TO, tormogen cell; TR, trichogen cell. (Based on Bin *et al.*, 1989).

et al. 1993; Isidoro and Bin 1995) but have also been found in females (Bin *et al.* 1989). These glands occur in different locations and are thus classified accordingly. Some glands are associated with campaniform sensilla. Other glands are associated with multiporous gustatory sensilla and we

have considered them to be accessory glands to the MGS.

Female Dorsal Glands (FDG)

In female *Trissolcus basalis* shallow dorsal depressions are present on A7 to A11 (Fig. 10a, b). These depressions are the re-
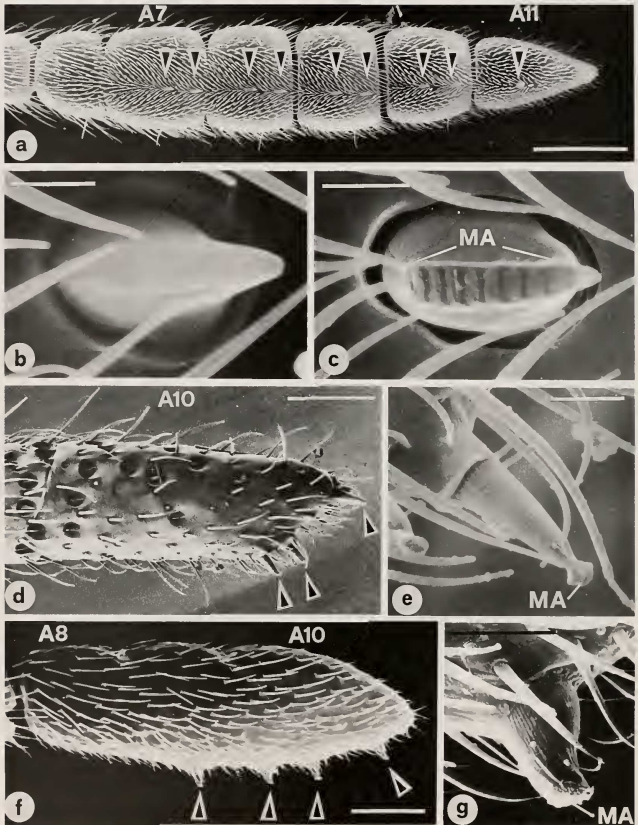
Fig. 4. Distribution of multiporous gustatory sensilla (arrows), in females of: a) *Trissolcus basalis*, ventral view; b) and c) single MGS before and after protease treatment respectively; d) and e) *Mantibaria anomala*, lateral view; f) and g) *Amitus spiniferus*, lateral view. MA, multiporous area. (bars: a = 50 micron, b and c = 2 micron, d and f = 25 micron, e and g = 5 micron).
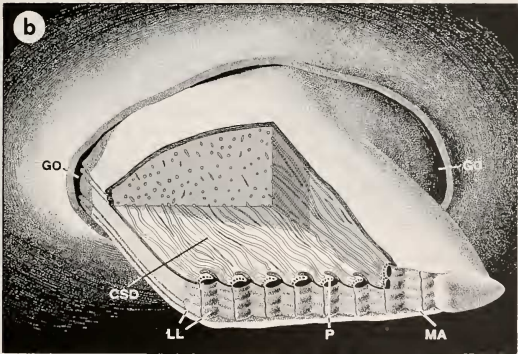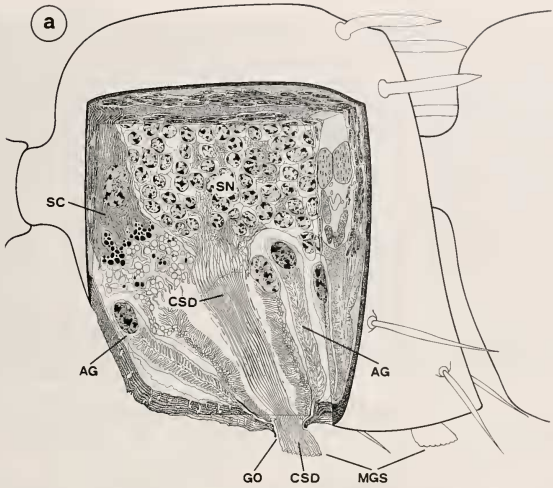
Fig. 5. Semischematic representation of multiporous gustatory sensilla (MGS) and associated accessory glands (AG) in *Trissolcus basalis*: a) internal view of a subapical antennomere, b) detail showing the multi-porous area (MA). CSD, chemosensory dendrites; GO, glandular outlet; LL, liftable lobes; P, pores; SC, sheath cells. (Adapted from Bin *et al.*, 1989).
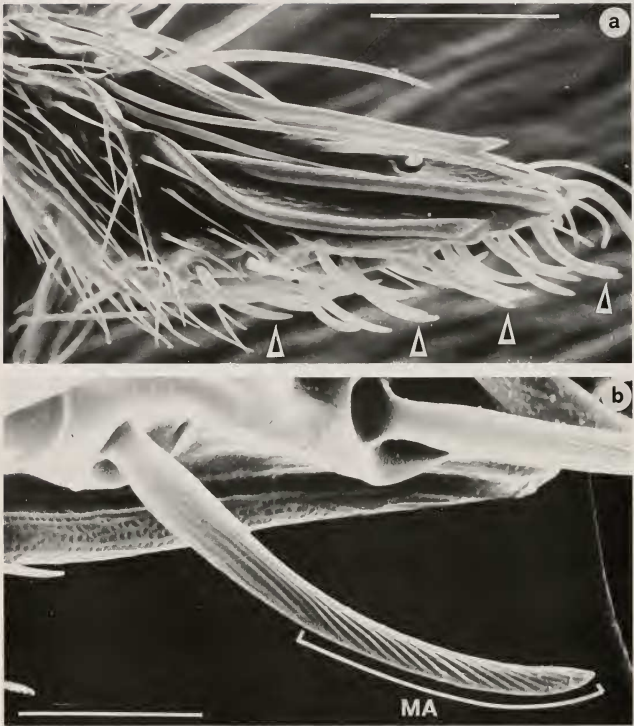
Fig 6. Multiporous gustatory sensilla (some arrowed) of *Trichogramma brassicae* female: a) lateral view of apical antennomere, b) detail showing the multiporous area (MA). (bars: a = 25 micron, b = 5 micron).

lease sites of a series of extensive glands (Bin *et al.* 1989) forming a longitudinally elongated cluster of about 20 unicellular secretory units that correspond to class 1 gland cells of Noirot and Quennedey (1974, 1993) (Fig. 11a). The internal wall of the dorsal depression shows pores which correspond to the irregular outlets of the glands (Fig. 10c). The associated campaniform sensillum, visible from both an external and internal view (Fig. 10b, c) is innervated by a single sensory neuron whose dendrite terminates in a typical tubular body (Bin *et al.* 1989) (Fig. 11a).
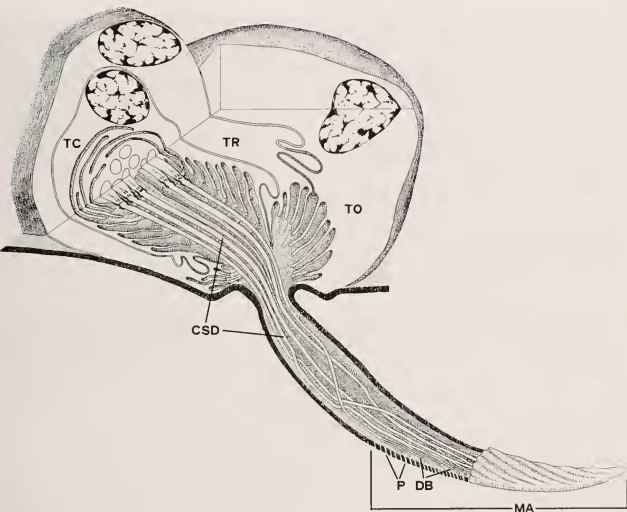
Fig. 7. Semischematic drawing of multiporous gustatory sensillum of *Trichogramma brassicae* female. CSD, chemosensory dendrites; DB, dendritic branches; MA, multiporous area; P, pores; TC, tecogen cell; TO, tormogen cell; TR, trichogen cell.

A similar type of gland is found in female *Trissolcus simoni*, but in this species the release sites are pits that occur on A4–A11 (Fig. 10d). Together with pits the campaniform sensilla are easily visible both externally (Fig. 10e) and internally (Fig. 10f). A dorsal gland in the antennae of *Amitus spiniferus* occurs in A8–A10, the claval segments being fused. This gland extends the length of the clava and occupies the dorsal half of the antennomeres (in preparation).

Another new case of these glands has been found in an aculeate parasitoid, the dryinid *Neodryinus typhlocybae*. In this species the antennomeres involved are A5 to A10. The glands belong to class 1 (in preparation). The conspicuous external structure is composed of 4 longitudinal deep grooves each incorporating a longitudinal lamina (Fig. 23a, b). These grooves have erroneously been thought to be sensilla and named rhinaria (Olmi 1984, 1994).

The function of the dorsal glands are not clear but, as described below, we suggest they play an important role in sex recognition.

MGS Accessory Glands (AG)

These glands can be found associated with a single multiporous gustatory sensillum, as in *Trissolcus basalis*, or with a group of sensilla, as in *Trichopria* (probably *drosophilae*). In both situations the glands belong to type 1. In the first case there is at least a couple of glands per sen-
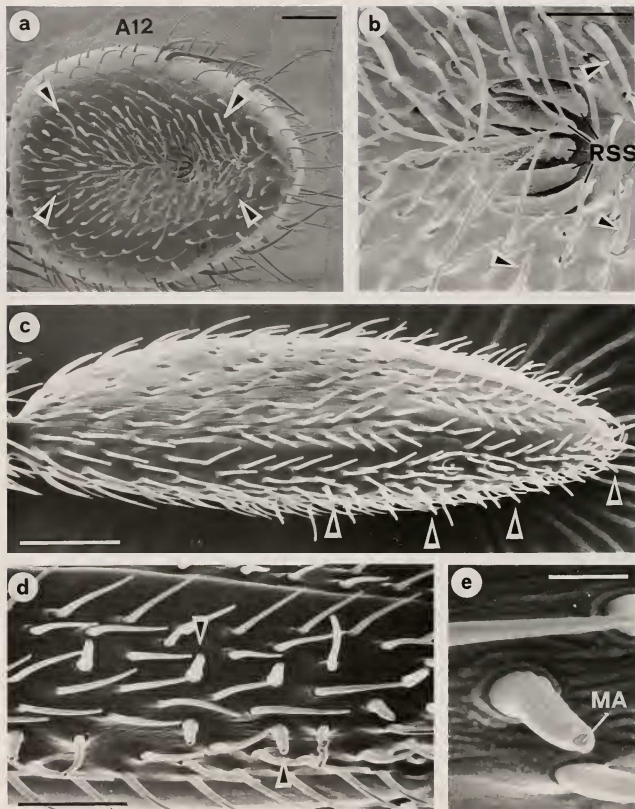
Fig. 8.   Ventral view of apical antennomere in *Trichopria* (probably *drosophilae*) showing: a) area with MGS interspersed with trichoid sensilla (arrowed), b) detail with some MGS (arrowed) surrounding the release and spread structures (RSS). Suspected multiporous gustatory sensilla (some arrowed) of *Polynema striaticorne* female: lateral view (c) and ventral view (d) of apical antennomere; e) detail showing the possible multiporous area (MA). (bars: a and c = 25 micron, b and d = 10 micron, e = 2 micron).
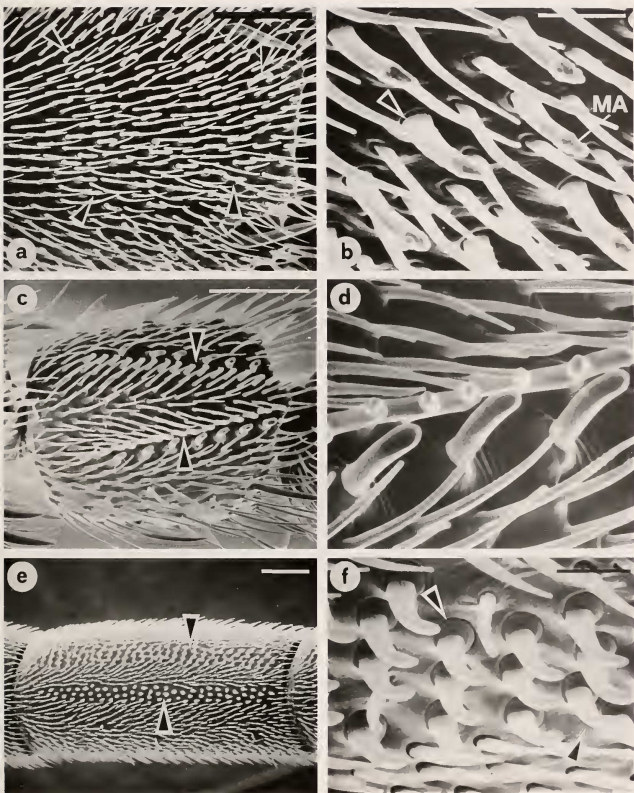
Fig. 9.　Suspected multiporous gustatory sensilla (some arrowed) in ventral view of a-b) *Coptera occidentalis*, c-d) *Aphanogmus steinitzi*, e-f) *Neodryinus typhlocybae*. MA, possible mulitporous area. (bars: a, c and e = 25 micron, b = 10 micron, d and f = 5 micron).
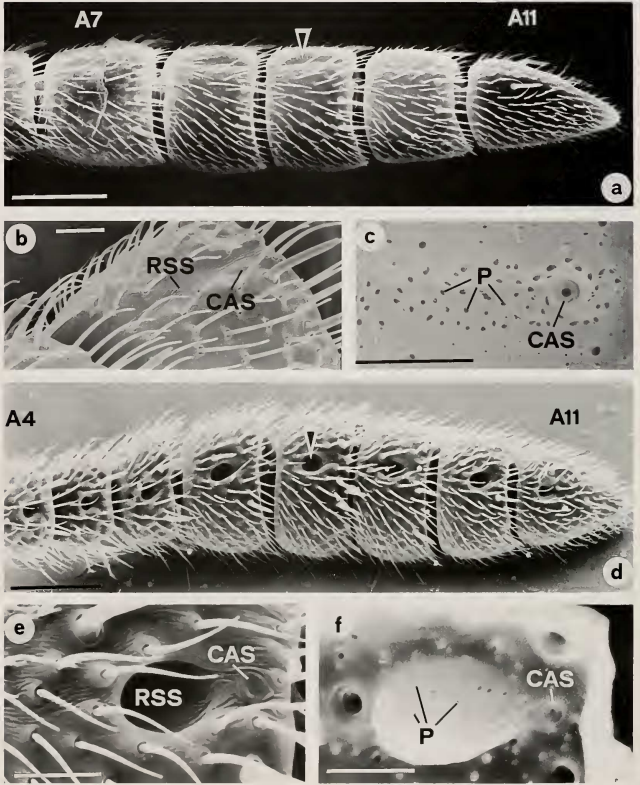
Fig. 10. Release and spread structures (RSS, one arrowed) of female dorsal glands in *Trissolcus basalis:* a) distribution in dorso-lateral view; b) details of external view with a campaniform sensillum (CAS) and c) corresponding internal view . The same in *Trissolcus simoni* (d-f). P, pores. (bars: a and d = 50 micron, b, c, e and f = 10 micron).
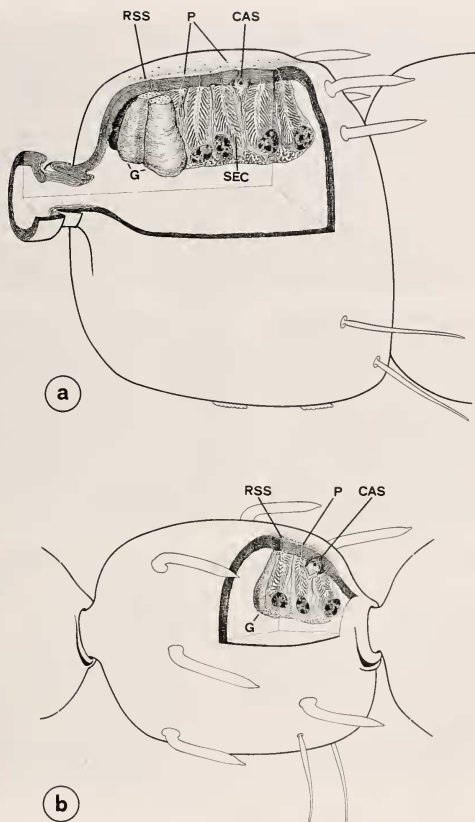
Fig. 11. Semischematic drawings of female (a) and male (b) dorsal glands of *Trissolcus basalis*. CAS, campaniform sensillum; G, gland; P, pores; RSS, release and spread structures; SEC, secretory cells. (Based on Bin et al., 1989).
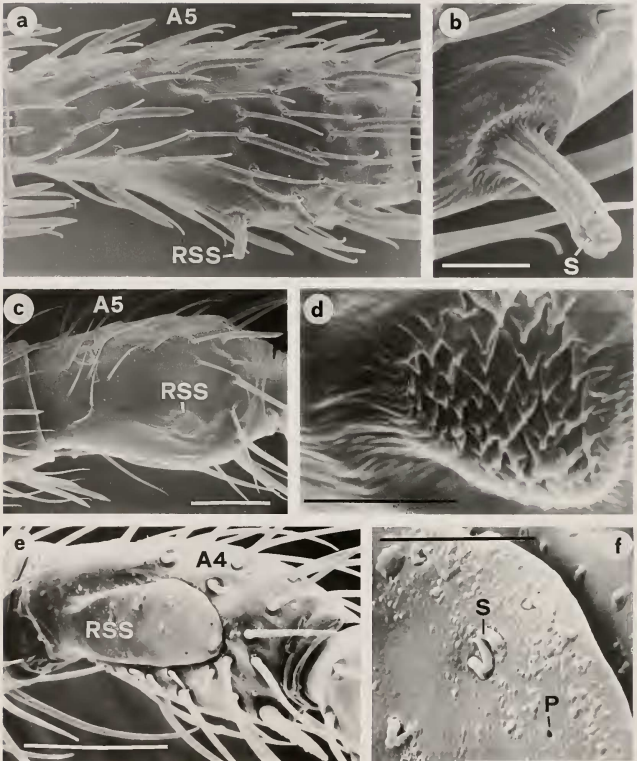
Fig. 12. Release and spread structures (RSS) of male ventral gland in: a-b) *Trissolcus basalis*; c-d) *Telenomus chloropus*. The same of male lateral gland (e-f) in *Amitus spiniferus*. S, secretion; P, pore. (bars: .a, c and e = 25 micron, b, d and f = 5 micron).

sillum having their outlets in the socket (Fig. 5) so that the secretion covers the multiporous area obscuring the cuticular ultrastructure (Fig. 4b) unless removed with proteolytic enzyme (Fig. 4c) (Bin *et al.* 1989). In the second case shown by *Trichopria* (probably *drosophilae*) 5–6 glands open in the center of the apical antennom-
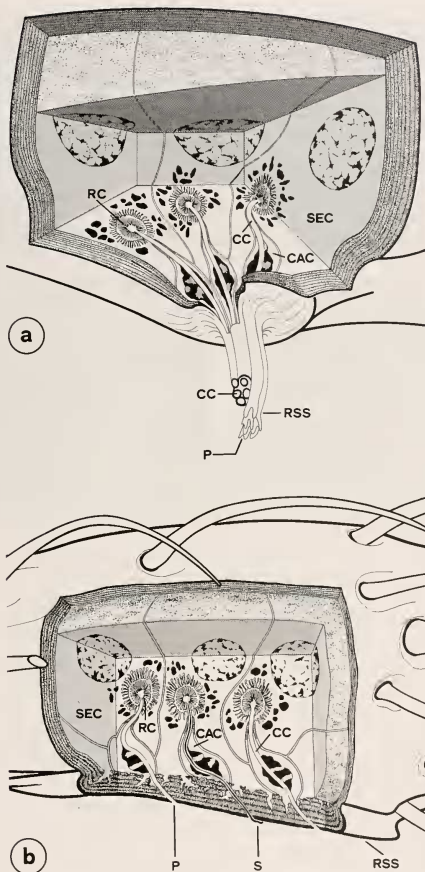
Fig. 13. Semischematic drawings of male ventral gland, lateral view, of *Trissolcus basalis* (a) and male lateral gland, dorsal view, of *Amitus spiniferus* (b). CAC, canal cell; CC, conducting canal; P, pore; RC, receiving canal; RSS, release and spread structure; SEC, secretory cell. (a: based on Bin & Vinson, 1986; b: based on Isidoro and Bin 1995).
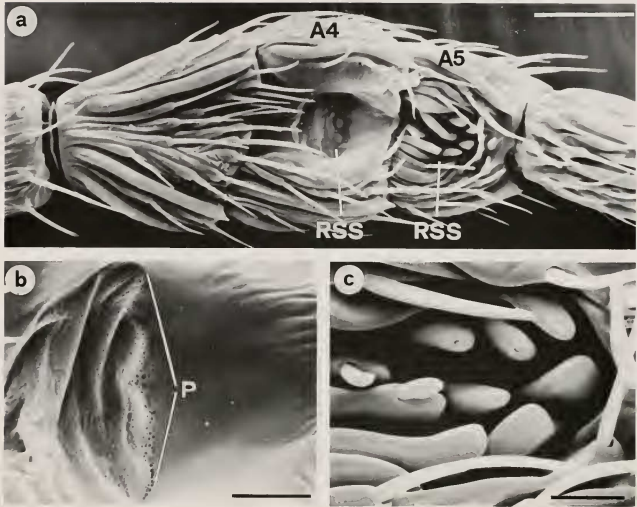
Fig. 14. Release and spread structures (RSS) of male ventral glands in *Encarsia asterobemisiae* (a) of different type in A4 (b) and A5 (c). P, pores. (bars: a = 25 micron, b and c = 5 micron).

ere (A12) (Fig. 8a, b) through 5–6 sub-conical porous structures located in a shallow depression surrounded and partially covered by MGS and setae (in preparation).

Although the role of the glands is not clear, a hypothesis is discussed in the section on "release and spread area".

Male Dorsal Glands (MDG)

Male *Trissolcus basalis* have antennal glands located in the dorsal distal region of A6-A11 but no obvious cuticular structure appears with SEM observations. Only ultrastructural investigations show that the glands are of type 1 and small in size (Bin *et al.* 1989) as diagrammed in Fig. 11b. It also appears they are associated with a campaniform sensillum.

Male Ventral and Lateral Glands (MVG and MLG)

These two types of glands may belong to the type 1 or 3, depending on the different taxa.

In the scelionid *Trissolcus basalis* the ventral gland on the modified A5 antennomere has an apparent release site consisting of a cylindrical peg, longitudinally fluted, and inserted in a shallow depression (Fig. 12a, b). The tip of the peg (the release site of the gland) when treated with protease shows 8–10 openings. Internally the gland consists of 8–10 isolated bicellular secretory units each formed by a secretory cell, corresponding to class 3 gland cells, and a canal cell forming the
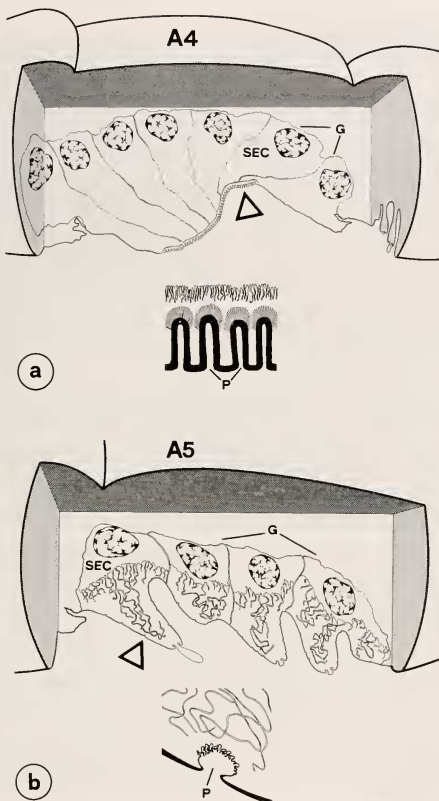
Fig. 15. Semischematic drawings of the two different types of male ventral glands in *Encarsia asterobemisiae*. Pores (arrows) of the two different release and spread structures in insets. G, glands; P, pores; SEC, secretory cell (based on Pedata *et al.* 1993).
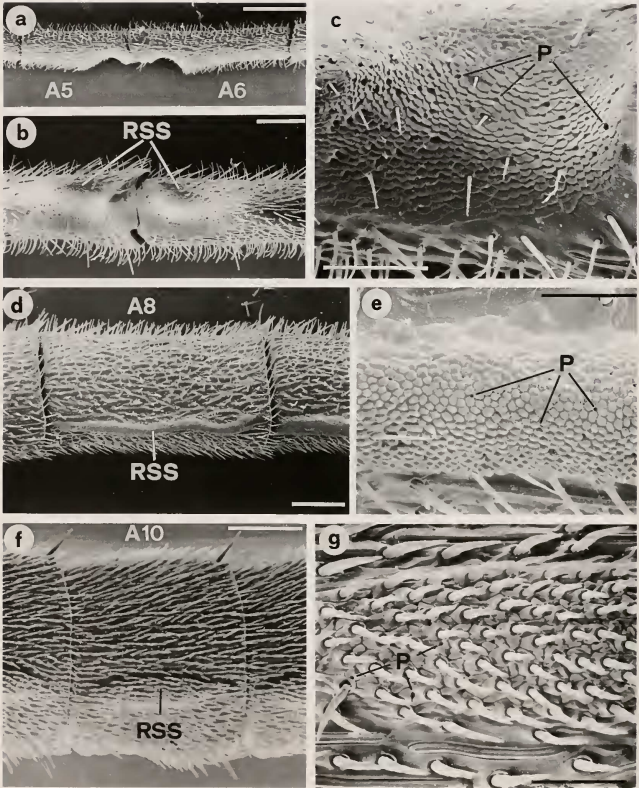
Fig. 16. Suspected release and spread structures (RSS) of male glands in some Ichneumonidae: a-c) *Cylloceria melancholica*; d-e) *Pimpla hypocondriaca*; f-g) *Ichneumon sarcitorius*. P, pores. (bars: a = 250 micron, b, d and f = 100 micron, c = 50 micron, e and g = 25 micron).

Fig. 17. Hypothetical female antenna with distribution of ascertained and supposed multiporous gustatory sensilla (MGS) in different taxa: a) apical and/or apico-ventral area, b) ventral area involving several antennomeres, c) ventral area involving many antennomeres. Aph, Aphelinidae; Bra, Braconidae; Cer, Ceraphronidae; Dia, Diapriidae; Dry, Dryinidae; Enc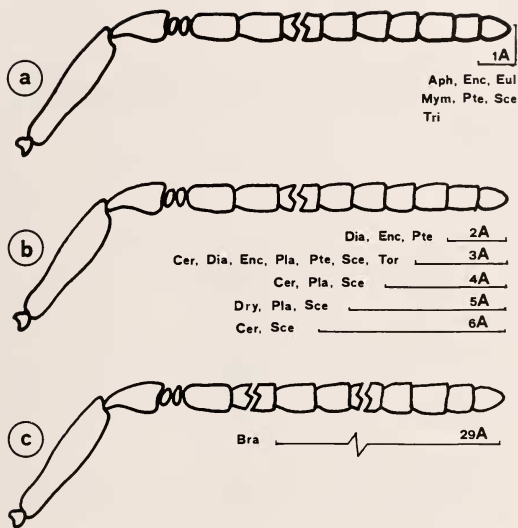, Encyrtidae; Eul, Eulophidae; Ich, Ichneumonidae; Mym, Mymaridae; Pla, Platygastridae; Pte, Pteromalidae; Sce, Scelionidae; Tri, Trichogrammatidae; Tor, Torymidae.

conducting canal which connects the receiving canal to the external glandular opening (Fig. 13a) (Bin and Vinson 1986).

The release site in not always an obvious peg. For example on another scelionid the gland opens on the surface of the antennomere (Fig. 12d), but is even less obvious when covered by secretion (Fig. 12c). In the platygastrid *Amitus spiniferus* there is a lateral gland on modified A4 with an external release site in form of a glabrous elevated plate elliptical in shape and with about 20 scattered pores (12e, f). Internally, the gland consists of some 20 isolated bicellular secretory units similar

in structure to those observed in the male ventral gland of *Trissolcus basalis* (Fig. 13b) (Isidoro and Bin 1995).

In the aphelinid *Encarsia asterobemisiae* there are two ventral glands on modified A4 and A5 (Fig 14a). Externally the ventral side of A4 has a deep cavity with the bottom and the proximal wall perforated by numerous pores (Fig 14b), whereas the A5 has a concave area with 9 subconical cuticular projections (7 with a small spherical structure on the tip and 2 with a spatulate structure) (Fig. 14 c). Internally, the two different release sites correspond to two integumentary glands, both belong-
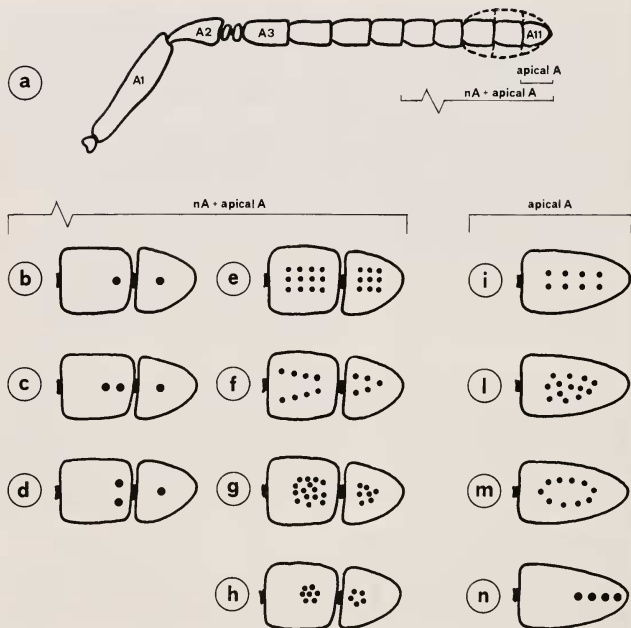
Fig. 18. Hypothetical female antenna (a) and distributional patterns of ascertained and supposed multiporous gustatory sensilla in different taxa: b) single, c) single and parallel pairs, d) single and transverse pairs, e) triple row, f) double row convergent, g) scattered, h) clustered, i) double row, l) scattered, m) elliptical, n) single row.

ing to the class 1 gland type, but with different cytological features (Fig. 15) (Pedata et al. 1993).

FUNCTIONAL AREAS AND THEIR POSSIBLE BIOLOGICAL ROLE

The lack of anatomical studies of the antennal sensilla and other antennal structures or antennal regions has led to a presumption of a sensory function for these structures. Further, the diversity in the ex-

ternal morphology has resulted in a diversity of terms for these structures and regions. Thus, attempts to associate functions with receptor morphology have been predicated on an assumed sensory function. The realization that some of these structures are secretory and others are sensory along with common associations between these two, suggests a functional region may exist. We are here proposing a new terminology in the attempt to com-
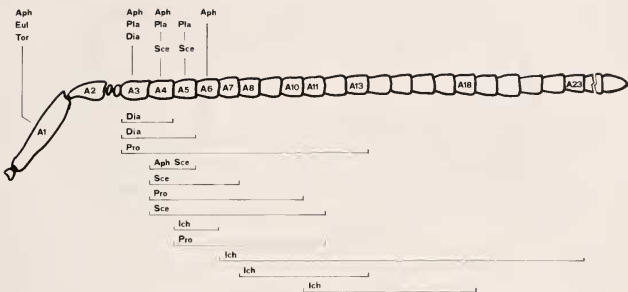
Fig. 19. Hypothetical male antenna with distribution of ascertained and supposed antennal glands in different taxa. Taxa having only one antennomere with gland are indicated above the antenna, those with more than one are reported below. Aph, Aphelinidae; Dia, Diapriidae; Eul, Eulophidae; Ich, Ichneumonidae; Pla, Platygastridae; Pro, Proctotrupidae; Sce, Scelionidae; Tor, Torymidae.

bine the new data illustrated above with the behavioral observations available from the literature.

"Touch and Taste Area"

The occurrence of non-volatile chemicals preceived by the antennae which are important in host recognition have been described for a number of species of parasitoids (Vinson 1985, 1991). Similarly, non-volatile chemicals have been isolated from the braconid, *Cardiochiles nigriceps* Viereck, that are produced by females which only elicit sexual behavior in males on contact (Syvertsen et al. 1995). Thus, touch and "taste" appears to be important in both host and mate recognition.

The touch and taste area can be defined as an area of an antennomere or series of antennomeres that is associated with one or more gustatory sensilla. This definition includes both uniporous (UGS) and multiporous gustatory sensilla (MGS) which have to "touch" the active compound/s in order to "taste" the proper chemical stimuli. Further, the UGS, being equipped with a mechanoreceptor, can also perceive a mechanical stimulus while the MGS can-

not. The "area" is the portion of antennomere/s bearing one of this type of sensilla. Examples of "touch and taste areas" are documented here. In regards to UGS, this functional area can be found in both sexes. The functional area may be only the tip of the apical antennomere or may consist of the ventro-lateral side of several antennomeres. In contrast the touch and taste area involving the MGS are found only in females, either on the tip of the apical antennomere or ventrally on several antennomeres. These latter sensilla are, however, surrounded by numerous tactile trichoid sensilla, all oriented ("combed") towards the midline and the MGS, or they are interspersed with them.

Touch and taste areas involving UGS are present in *Encarsia asterobemisiae* (Fig. 3a), *Trissolcus basalis* (Fig. 3b), and *Amitus spiniferus* (Fig. 3c). Together the MGS, which lack mechanical receptivity, and the tactile sensilla form a touch and taste area as shown by MGS found in *Mantibaria anomala* (Fig. 4d–e; Fig. 18n), *Trissolcus basalis* (Fig. 4a–c; Fig. 18c), *Amitus spiniferus* (Fig. 4 f–g; Fig. 18c), *Trichogramma brassicae* (Fig. 6a; Fig. 18l) and *Coptera occiden-*
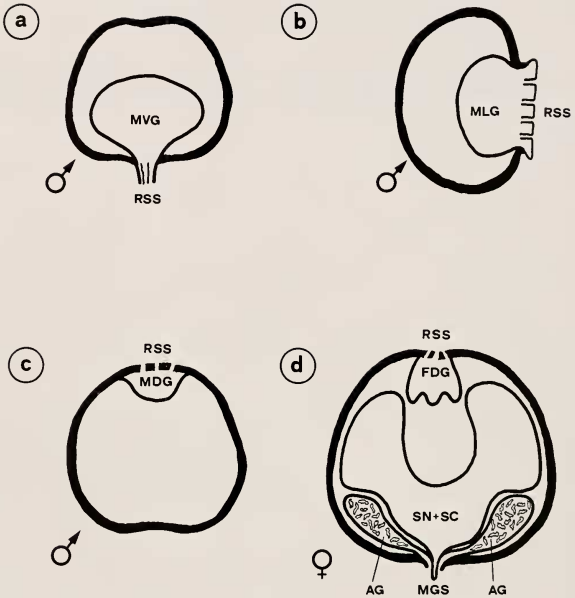
Fig. 20. Semischematic drawings of transverse sections of male (a, b, c) and female (d) antennomere showing localization and relative volume of glands and sensory neurons with sheath cells (SN + SC) of multiporous gustatory sensillum (MGS) (a, c, d: *Trissolcus basalis*; b: *Amitus spiniferus*). AG, accessory glands; FDG, female dorsal gland; MDG, male dorsal gland; MLG, male lateral gland; MVG, male ventral gland; RSS, release and spread structure.

talis (Fig. 9a–b; Fig. 18g). The evidence for a touch and taste area involving the MGS in the scelionid *Trissolcus basalis* and the platygastrid *Amitus spiniferus*, can conceivably be extended to the whole superfamily Platygastroidea. There are a number of authors who have focused on parts of the antennae, which we now refer to the "touch and taste area". Referring to these either as indefinite or as abrupt clava, or referring to a specific sensillar formula

(Bin 1981; Masner 1976; Masner and Huggert 1989), including the unique case of the genus *Nixonia* Msn. (Masner and Huggert 1989) (Fig. 18d). Further, we provide evidence (Fig. 18l) that the basiconic sensilla in *Trichogramma brassicae* are MGS forming a "touch and taste area" or "sole chercheuse" (= searching sole) proposed for *Trichogramma* species (Voegele *et al.* 1975; Olson and Andow 1993). In the diapriid *Trichopria* (probably *drosophilae*), a
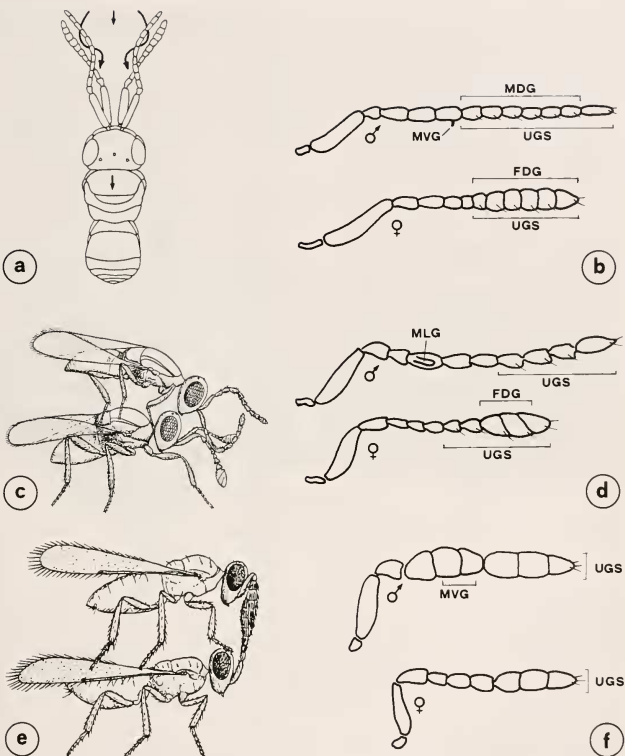
Fig. 21.   Suggested correlations between uniporous gustatory sensilla (UGS) and glands in sexual recognition. Precopulatory phase in a) *Trissolcus basalis*, c) *Amitus vesuvianus*, e) *Encarsia asterobemisiae*. Semischematic drawings of male and female antennae in *T. basalis* (b), *Amitus spiniferus* (d), and *E. asterobemisiae* (f). FDG, female dorsal gland; MDG, male dorsal gland; MLG, male lateral gland; MVG, male ventral gland. (c: from Viggiani and Battaglia, 1983a; e: from Viggiani e Battaglia, 1983b).
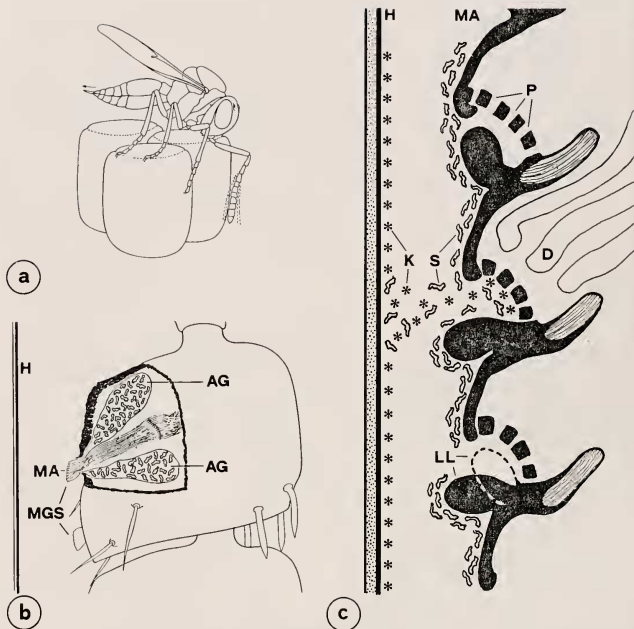
Fig. 22. Possible role of multiporous gustatory sensilla (MGS) and accessory glands (AG) in host recognition of *Trissolcus basalis*: a) host examination by antennal drumming and rubbing; b) semischematic detail of host egg (H) and antennomere with MGS and AG; c) semischematic detail of host and multiporous area (MA) of MGS. D, dendrites; H, host; K, kairomone; LL, liftable lobe; P, pores; S, secretion.

group of MGS interspersed with tactile setae defines a ''touch and taste area'' in the two apical antennomeres of a three segmented clava (unpublished).

Several other examples of distinct areas with characteristic sensilla have been reported in females of several parasitoid families. These could fit the definition of ''touch and taste area'' when anatomical studies of the sensilla are available. All the traditionally described clavomeres and

probably many of the non-incrassate antennomeres may exhibit a ''touch and taste area'' ventrally or ventro-laterally. Dessart (1994) proposed the term ''thigmochore'' or touching area for a region of the antennae of ceraphronids distinguished by an area with trichoidea and basiconica sensilla, ''thigmomere'' for any flagellomere provided with such an area, and ''thigmus'' for the continuous or discontinuous antennal segments bearing

Fig. 23. Dorsal view of female antennomere 8 (A8) showing the release and spread structures (RSS) of dorsal glands in *Neodryinus typhlocybae* (a, b). Ventral view of male antennomere 10 (A10) with a couple of release and spread structures (RSS) in *Vespa crabro* (bars: a, b, and d = 25 microns, c = 250 microns).
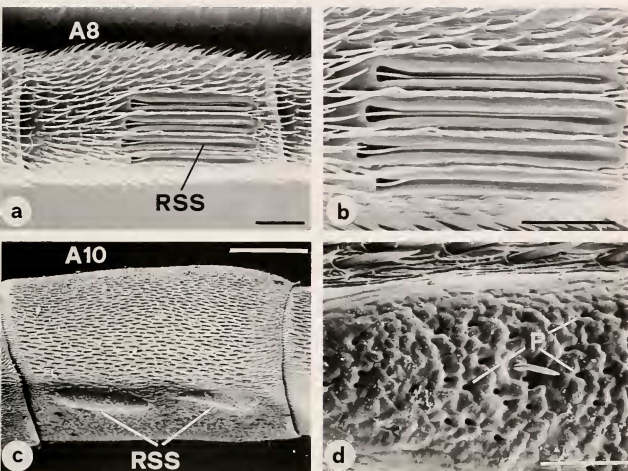
thigmomeres. However, the presence of gustatory sensilla important in the detection of contact chemical cues (Vinson 1991) suggests a taste function as well. Some other possible examples of a "touch and taste area" involving gustatory and tactile sensilla include the following. In the mymarid *Polynema striaticorne* the clava exhibits a double row of blunt tip basiconic sensilla which likely have a multiporous tip (Fig. 8c-e, 18i). In Pteromalidae the clava has often an area of finer or at least different pilosity, usually collapsing in dry specimens, called the "micropilosity area" (Graham 1969; Boucek 1988). In some pteromalids (Miller 1972) the micropilosity area can be defined by thick-walled chemoreceptors. For some aphelinids the term "claval sensorial complex"

has been proposed, suggesting a host or mate recognition function (Polaszek and Hayat 1992). In some encyrtids the "sensory part of clava" is indicated by an area of micropilosity or microtubules or a sieve-plate structure which may be limited to the extreme apex of the antennae or extended almost to the base (Noyes and Hayat 1994). In other encyrtids the tip of the antenna is flattened and bears sensilla located in an elliptical pattern (Weseloh 1972; Domenichini 1977–78) (Fig. 18m). A torymid has patches composed of several fluted basiconic sensilla terminating apically in a small bulb-like structure (Domenichini 1977–78) which could be multiporous gustatory sensilla. These basiconica sensilla are likely multiporous gustatory sensilla arranged in different

patterns, triple row, double convergent rows, large patches (Fig. 18e,f,g) and at least in one case (Fig. 9c,d) could be of two different types. In the dryinid *Neodryinus typhlocybae* the ventral side of the 6 distal slightly thickened antennomeres presents short apically bent and flattened basiconic sensilla located in two longitudinal parallel bands, each composed of two-three rows (Fig. 9e, f). These could be multiporous gustatory sensilla (in preparation). Even the braconid *C. nigriceps* has fluted bent-tipped basiconic sensilla on the apical antennomere and the preceding 28, all appearing to contact the substrate during host searching (Norton and Vinson 1974a, 1974b).

Ascertained and suspected "touch and taste areas" are summarized in Fig. 17 which shows how the antennomeres involved may greatly vary in number between and within the groups, and are concentrated in the distal portion of the antenna. The functions of the "touch and taste areas" are likely correlated with intra- or interspecific communication, i.e. sexual or host recognition and discrimination, respectively.

"Release and Spread Area"

This term suggests a double function for some cuticular structures which, while they "release" the gland secretion through pores, also may "spread" the secretion onto the proper sensilla or surface, or at least make contact with them. The "area" refers to single or numerous antennomeres, modified or unmodified, bearing any type of a "release and spread structure" (RSS), apparent or inconspicuous. The location of RSS reflects that of the respective glands, i.e. dorsal, ventral or lateral (Fig. 20a–d). All the glands listed in the previous section have a more or less characteristic RSS, including the special case of accessory glands (AG) which are associated with the MGS in some species (Fig. 20d).

The RSS connected with female dorsal glands (FDG) appear as shallow depressions in *Trissolcus basalis*, from A7 to a11 (Fig. 10a–b), or as deep pits in *Trissolcus simoni*, from A4 to A11 (Fig. 10d–e). The RSS are inconspicuous on A8-A10 of *Amitus spiniferus*. In an internal view of RSS in both species of *Trissolcus* the pores that penetrate the cuticular wall become apparent together with an opening associated with the campaniform sensillum (CAS) (Fig. 10b–c, e–f; 11a).

The release site of MGS accessory glands (AG) in *Trissolcus basalis*, is located in the sensillum socket (Fig. 5a–b; 20d). It seems logical that the spreading function be performed by the multiporous area at the tip of the sensillum which, in fact, appears to be covered by abundant secretion (Fig. 4b). What the general situation is within a family or superfamily, cannot be determined as yet since the scelionid *Telenomus busseolae* has an AG, whereas we have no evidence of such a gland in another scelionid, *Mantibaria anomala*, or the platygastrid *Amitus spiniferus* (in preparation). Therefore, the presence of MGS does not necessarily imply the existence of accessory glands.

The inconspicuous RSS of the male dorsal glands (MDG) in *Trissolcus basalis*, the only species for which such structures in males described so far (Bin *et al.* 1989), does not differ from the surrounding sculpture which includes the associated campaniform sensillum (CAS) (Fig. 11b).

In contrast, a great variety of RSS have been described for the male ventral (MVG) and lateral (MLG) glands, having been noticed for their appearance, but until recently (Dahms 1984, Bin and Vinson 1986, Bin and Isidora 1995, Pedata *et al.* 1995) confused with sensory organs. The RSS are often associated with variously modified antennomeres but also occur on unmodified ones.

Among the scelionids a number of species have a single modified antennomere, A5, for a which a gland and a peg-like release structure has been described in one

species (Bin and Vinson 1986). All the others, whether having single or multiple modified antennomeres, (Waterston 1923; Ogloblin 1930; Masner 1976, 1980; Galloway and Austin 1984; Villa and Mineo 1990a, 1990b), also have specialized structures such as carine (keels), tyloids, plates, or pegs, which can be suspected to be release and spread structures.

In the aphelinids a variety of RSS may exist and, as shown (Figs 14, 15), may even differ on different antennomeres of the same species. In some species specialized structures have been found on A1 or other antennomeres that appear as lamellar projections (Viggiani *et al.* 1986) or conical processes (Viggiani and Ren 1991), short setae or pegs on A3 or A4 (Viggiani 1985, 1987), or a ventral plate bearing numerous minute setae on A6 (Rosen and DeBach 1979).

In males of many species, "sexually" modified antennomeres have been reported (see below).

In diapriids a modified antennomere with a longitudinal carina with a tooth or a pointed tyloid, can be found on A3, A4 or A5 depending on the subfamily. In Belytinae a modified antennomere can be found on A3 or, with only one exception, on A4 (Nixon 1957; Masner 1993). In Ambositrinae a modified antennomere can be found as A3 and A4, but sometimes also A5 (Naumann 1987; Masner 1993) and in Diapriinae A4 (Masner 1991) or a few cases occur with A3 and A4 (Silvestri 1913, Nixon 1957; Huggert and Masner 1983; Early and Naumann 1990). A doubtful case is a species of Diapriinae having A1 to A3 remarkably modified (Baudoin 1962).

In eulophids a glandular release and spread site is documented by Dahms (1984). Another spread and release site is suspected in *Aprostocetus* (=*Tetrastichus*) *hagenowii* because of the presence of a shallow trench at the center of A1 (Takahashi and Sugai 1982).

In platygastrids the only documented case of a gland refers to the elevated lateral plate of A4 (Isidoro and Bin 1995). In other members of the family the secretory function can be suspected when the antennomeres are strongly bent ventrally or are much longer than the others, such modifications also occurring on A3 or A5. The specialized structures can be plates (MacGown 1979), or longitudinal sharp ventral carina which in some cases end in a subapical tooth (Masner and Huggert 1989).

In proctotrupids, the species of a genus are nearly always provided with patches of specialised antennal structures (Nixon 1938) some of which have been called tyloids. These appear as slightly raised elliptical areas that may be hairless, polished or minutely punctate and vary in size depending on the length of the segments. They may involve several antennomeres up to the apical one (Townes and Townes 1981). In ichneumonids, as illustrated in Fig. 16, tyloids usually appear and vary in form, such as a longitudinal prominence (Richards 1956), an elliptic or linear raised area on the outer side of each of several antennomeres near the mid-length of the flagellum (Townes 1969), or as a porous keel (Frilli 1974). These tyloids may also be gland release structures.

In two torymid species A1 is broadened and strongly arched, with the ventral surface covered with small pores. This area of A1 appears to come into contact with the female flagella during courtship (Goodpasture 1975).

Besides the examples described above, there are a few others which are questionable because the antennomere is modified, but there is no obvious specialized structure. Examples of this situation occur in two groups; the Eucoilidae with A3 and/or A4 bent, the outer side flattened proximally and more or less swollen distally (Nordlander 1980), and the Heloridae with the posterior surface of A5 sinuate and smooth (Naumann 1983).

Based on identified RSS and those sus-

pected to be RSS, due to their morphology and location, we have developed a map (Fig. 19) of the location of RSS on a hypothetical male antenna. As can be seen on the map, the RSS may range from the scape, A1, to the most apical antennomere with a concentration in the proximal half of the antenna. The suspected secretory function may only occur in A1 in the Chalcidoidea (Aphelinidae, Eulophidae, Torymidae). These RSS may occur much more frequently in A3 to A5 in all the Superfamilies regardless of the antennomere number. However, the glands extend from A6 to several others in Scelionidae, Proctotrupidae and Ichneumonidae. In no case does A2 play this role. Multiple modified antennomeres with RSS may have a different functional significance or may simply be a multiplication of the same functional structure, possibly to allow for the enhancement of the stimulation or to allow for the induction of a more rapid response. An example of the first case is that of A4 and A5 in *E. asterobemisiae* (Pedata *et al.* 1995) which have different specialized structures associated with different glands which may play different roles in some complex behavior. The second seems to be the situation of some Scelionidae, Proctotrupoidea and Ichneumonidae because the repeated specialized RSS structures appear to be the same.

The term "sex segment" was proposed for the modified antennomere/s on the basis of their speculated involvement in mating behavior of scelionids (Masner 1976). Evidence of a role in mating behavior was later provided by Bin *et al.* (1988) for *Trissolcus basalis*. A similar term, male-sex antennomere (MSA) (Isidoro and Bin 1995), has also been used in a platygastrid being determined by ultrastructural evidence and some behavioral observations. The presence of modified antennomeres with release and spread structure (RSS) in males of various parasitoid groups strongly suggest a sexual recognition function. However, similar structure in females could function in either sexual recognition or host recognition, or both.

Sexual Recognition

All the documented cases listed above indicate that the "UGS touch and taste area", located apically or latero-ventrally, could be used for sexual recognition in conjunction with the female dorsal glands and male ventral or lateral glands and associated "release and spread areas".

The diversity of gland structure and location suggests a strong selection pressure towards a unique antennal glandular system in each species. It has been long recognized that the elaborate courtship behaviors in many parasitoid hymenoptera are very effective reproductive isolation mechanisms (Barrass 1979; van de Assem 1986, 1996). However, it is difficult to use a complex behavioral sequence involving two individuals as a taxonomic tool. The use of the glands may provide a key to reproductive isolation mechanisms in these insects. Further, the UGS pattern may also play a role in the sexual isolation. The secretion, if important in sex recognition, must be perceived by the opposite sex. Since the secretions appear to be non-volatile, as evidenced by the need to remove high molecular weight lipids and proteins to reveal details of the surface ultrastructure of many of these glands, and the presence of visible secretions (Fig. 12), they must be detected by a gustatory type of sensilla. Thus, the placement of the uniporous gustatory sensilla and the glands should reflect the behavior. Although details of the sexual recognition behavior of the parasitic Hymenoptera that consider the positions of the glands and sensilla have not been examined, with the exception of information concerning *Trissolcus basalis* (Bin *et al.* 1988; Bin and Vinson, unpub.), we suggest that such information could demonstrate the importance of the glands, sensilla, and behavior as a reproductive isolation mechanism. In *Trissolcus basalis*, males mount the female and en-

gage in elaborate antennal interactions (Fig. 21a) where the antennae of the male initially drums the female antennae. This places the male uniporous sensilla in contact with the female dorsal glands. As the antennation proceeds, the antennae of the male appears to coil partly around the antennae of the female, usually from the medial side (Fig. 21a). The male then moves back slightly, resulting in the sliding of the males antennae segment A5, along the inner lateral edge of segments A11 to A6 of the female where uniporous sensilla are located. Whether these glands and sensilla are involved in sexual recognition remains to be ascertained.

Some behavioral observations on *Amitus vesuvianus* and *A. rugosus* have shown that the male A4, having a lateral plate functioning as a release and spread structure very similar to that of *A. spiniferus* (Fig. 21d) (Isidoro and Bin 1995), touches the median side of the basal segments of the female funicle during courtship and mating (Fig. 21c) (Viggiani and Battaglia 1983a, 1983b).

Another example is provided by *E. asterobemisiae* where the behavior has been described by Viggiani (1980) (Fig. 21e). During the elaborate antennal interaction involved in sexual recognition, the reported glands and uniporous gustatory sensilla of the male seem to be appropriately positioned with the uniporous gustatory sensilla of the female. However, the role of uniporous gustatory sensilla of the male is uncertain because it is unknown whether a gland is present in these antennomeres of the female.

We suggest that correlating the location of secretory areas of the antennae with that of the uniporous gustatory sensilla, entering into contact during courtship, may provide valuable keys to some species specific sensilla and gland patterns. These aspects do not seem to have been considered in other groups of parasitoids (van den Assem 1996).

Host Recognition

The "MGS touch and taste area", which typically occurs ventrally, ventro-laterally or apically, could be a common feature of parasitoids. Such an area, consisting of MGS, mechanoreceptive sensilla and in some cases UGS and accessory glands, could be functionally responsible for host recognition and discrimination since MGS and possibly UGS could be capable to respond to host recognition kairomone and host marking pheromone.

At least in one case, that of *Trissolcus basalis*, it can be speculated that the accessory gland secretion may be important in the host recognition process (Fig. 22). Bin *et al.* (1993) reported that host eggs removed from the ovary prior to the addition of an adhesive were not recognized. However, once the adhesive layer was added to the egg chorion, the parasitoid responded (Fig. 22a). Using glass beads of similar size to host eggs, Bin *et al.* (1993) reported no response, but if the adhesive was added, females responded. Further, females only responded when the adhesive was present on a curved surface. The results suggest the adhesive contains a kairomone to which the female parasitoid responds only when encountered on a curved surface (Bin *et al.* 1993). Further, the adhesive was found to be composed of a slightly acidic muco-polysaccharide with some protein. Thus, the adhesive is very complex. Although we do not know what specific compound or component of the adhesive is responsible for the recognition of the object as a host, the glandular secretion of the antennae of the parasitoid may play an important role in this response (Fig. 22b). Several possible scenarios include the dissolving of the adhesive by the secretion releasing the recognition cue, enzymatic degradation of the adhesive that releases or produces the recognition cue, or the secretion may act as some sort of receptor protein (Fig. 22c).

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CONCLUSIONS

Antennal gustatory sensilla and several types of glands, have been documented in a relatively few species of parasitoid Hymenoptera, but we suggest, based on locations and external features, that such sensory and secretory structures may be common. While these sensory and secretory structures appear to differ in detailed structure, shape, size, number, location and distribution; there are similarities and patterns that indicate a common function.

The presence of such organs has also been determined in Aculeata, such as the multiporous gustatory sensilla and female dorsal glands in the Dryinidae (Fig. 23a, b) and male ventral "tyloids" with conspicuous pores, likely indicating a releasing role, in *Vespa crabro* (L.) (Fig. 23c, d). In addition, cuticular structures possibly playing a secretory role, based on the presence of evident pores, occur in males of several parasitoid families (Sapygidae, Tiphiidae, Mutillidae, Pompilidae, Sphecidae) and non parasitoid hymenopterans (Eumenidae, Andrenidae, Anthophoridae) (Pagliano *et al.* unpublished).

Whether sensilla and glands are interactive structures for sex communication or play a role in host recognition (a kind of a "lock and key system") are hypotheses which still need confirmation. It is our hope to stimulate others to examine the antennae of the hymenoptera, not just as a sensory receiving organ, but as an organ that can be involved in the release of secretions. While the role of these secretions is speculative, we suggest they may be involved in sexual communication and in a few cases along with the gustatory sensilla, aid in host recognition. Assuming that the secretions are involved in sexual communication and the gustatory sensilla are involved in either sexual communication, host recognition, or both; mapping of these particular structures may provide for some taxonomic advance. Consideration of the glandular function and the an-

tennae and the presence of gustatory sensilla along with additional anatomical studies and behavioral observations focused on these structures may help to reinterpret antennal function, define homologies, unify terminology and provide additional information regarding phylogeny.

ACKNOWLEDGMENTS

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